The Ecology, Behavior, and Biological Control Potential of Hymenopteran Parasitoids of Woodwasps (Hymenoptera: Siricidae) in North America

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ABSTRACT   Native and exotic siricid wasps (Hymenoptera: Siricidae) can be ecologically and/or economically important woodboring insects in forests worldwide. In particular, *Sirex noctilio* (F.), a Eurasian species that recently has been introduced to North America, has caused pine tree (*Pinus* spp.) mortality in its non-native range in the southern hemisphere. Native siricid wasps are known to have a rich complex of hymenopteran parasitoids that may provide some biological control pressure on *S. noctilio* as it continues to expand its range in North America. We reviewed ecological information about the hymenopteran parasitoids of siricids in North America north of Mexico, including their distribution, life cycle, seasonal phenology, and impacts on native siricid hosts with some potential efficacy as biological control agents for *S. noctilio*. Literature review indicated that in the hymenopteran families Stephanidae, Ibaliidae, and Ichneumonidae, there are five genera and 26 species and subspecies of native parasitoids documented from 16 native siricids reported from 110 tree host species. Among parasitoids that attack the siricid subfamily Siricinae, *Ibalia leucospoides ensiger* (Norton), *Rhyssa persuasoria* (L.), and *Megarhyssa nortoni* (Cresson) were associated with the greatest number of siricid and tree species. These three species, along with *R. lineolata* (Kirby), are the most widely distributed Siricinae parasitoid species in the eastern and western forests of North America. Depending upon certain abiotic and biotic factors, we hypothesize that these four parasitoid species may contribute to the biological control of *S. noctilio*. Major gaps exist regarding parasitoid ecology, including their taxonomy, distribution range, exact siricid and tree hosts, interactions with hosts, phenology, and chemoecology in forest stands. As *S. noctilio* continues to expand its distribution in North America, a better understanding of the biology of these parasitoids may be needed in conifer-dominated landscapes.

KEY WORDS   *Ibalia*, *Megarhyssa*, *Pseudorhyssa*, *Rhyssa*, *Sirex noctilio*

Woodwasps or siricids (Hymenoptera: Symphyta: Siricidae) are subcortical insects that have a worldwide distribution, primarily north of the equator, and can be ecologically important, economically important, or both (Benson 1943, Stillwell 1966, Morgan 1968, Schiff et al. 2006). At present, ≈100 siricid species in two subfamilies and 11 genera are reported worldwide, including tropical areas of New Guinea, Philippines, Vietnam, Cuba, and the northern regions of India, Central America, and Africa (Schiff et al. 2006). Native siricids are unknown from Australia and South America (Smith and Schiff 2002). In North America (north of Mexico), there are two subfamilies of siricids: 1) Siricinae, which develops on many species of coniferous trees; and 2) Tremicinae, which develops on hardwood trees. Siricinae are most common in pines (*Pinus* spp.), but they also attack fir (*Abies* spp.), Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], incense-cedar (*Libocedrus decurrens* Torr.), spruce (*Picea* spp.) and tamarack (*Larix* spp.) trees. The five siricid genera present in North America are *Eriotremex*, *Sirex*, *Tremex*, *Urocerus*, and *Xeris*. There are 23 species within these five genera present in North America, including native (e.g., *S. nigricornis* F. and *U. cressoni* Norton) and non-native species, such as *S. noctilio* F. and *E. formosanus* (Matsumura).

Ecology of the Siricidae. Most siricid species have a complex tri-trophic interaction with the host tree and a symbiotic fungus (Morgan 1968, Kukor and Martin 1983). The life-cycle of siricids is typically 1–3 yr, with females ovipositing in the tree trunk and the larvae tunneling into the wood or xylem (Middlekauff 1960, Stillwell 1967, Schiff et al. 2006). Siricids have a haplodiploid sex determination system, where unmated females lay only haploid males, and mated females can lay both diploid males and females. While ovipositing, the female siricids (except species in the genus *Xeris*) also inoculate the tree with a symbiotic fungus that breaks down wood (Francke-Grosmann 1939, Graham 1967, Morgan 1968), and in the case of *S. noctilio*,

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reduces tree vigor (Slippers et al. 2003). Developing siricid larvae presumably feed on the fungi, decomposing wood, or both, and can have many instars (e.g., up to 12 have been reported for *S. noctilio*) (Madden 1981, Neumann and Minko 1981). Larvae pupate in the wood, and emerge as adults in midsummer and early fall, respectively, in the northeastern and southeastern United States through a distinctively round exit hole (Gandhi et al. 2010). Adult Siricidae are large, sexually dimorphic, and colorful insects allowing for relatively easy identification (Schiff et al. 2006). Adult Siricidae may show large size variation, have a broad waist, are stingless with a dorsal spine called a cornus on the last abdominal segment (hence, siricids are also called "horntails"), and females have a well-developed ovipositor. Adult males typically emerge from the wood first and fly with other males to trees higher in the canopy; this behavior is called lekking (Schiff et al. 2006). Females emerge soon afterwards and fly up to the males, mate, and oviposit on suitable host trees, starting the life-cycle again (Schiff et al. 2006).

Generally, siricid species in their native habitats are secondary colonizers attacking trees that are weakened and/or dying because of abiotic (e.g., smog, wildfires, or windthrow) and biotic (e.g., after being colonized by primary bark and other woodboring insects) factors (Cameron 1963, 1968; Spradbery and Kirk 1978; Gandhi et al. 2009). Native siricids occasionally can cause damage to cut logs (Wilson 1962). Native siricids may be ecologically important as they assist with the breakdown and decomposition of coarse-woody debris (Middlekauff 1960, Spradbery and Kirk 1978) and hence, contribute to nutrient cycling. However, some non-native species, especially *S. noctilio*, may be economically important as they can attack live trees and contribute to tree mortality (Rawlings 1948, Madden 1988, Iede et al. 1998). Tree health is adversely affected through both the activities of larvae boring into the xylem of the tree and by the symbiotic fungus clogging the vascular system (Madden 1977). Some siricid species, such as *S. noctilio*, also may inject the tree with phytotoxic mucus that adversely affects the tree's physiology, thus contributing toward further tree decline (Spradbery 1973, Madden 1977, Bordeaux and Dean 2012). However, not all non-native Siricidae are threatening North American forests (e.g., *E. formosanus*) now is found in 10 southeastern States, and has not caused any forest damage (Smith 1996, Warriner 2008).

Sirex noctilio is a native woodwasp species in Europe, Asia, and North Africa. It has been introduced to Argentina, Australia, Brazil, Chile, New Zealand, South Africa, Uruguay, and more recently to the United States and Canada (Carnegie et al. 2006, Hurley et al. 2007). The first discoveries of *S. noctilio* in New York and Ontario, Canada were found in 2004 and 2005, respectively (Hoebeke et al. 2005, de Groot et al. 2006), although it had been detected previously at various ports-of-entry in the United States (Hoebeke et al. 2005). Since 2005, established populations also have been found in Connecticut, Michigan, Ohio, Ontario (Canada), Pennsylvania, Quebec (Canada),

and Vermont, and it continues to expand its range in North America (NAPIS 2011). In the non-native range in the southern hemisphere, *S. noctilio* has been found to be a major pest of planted pine species, especially under drought conditions (Rawlings 1948). Major changes in forest management practices were implemented because of infestations by *S. noctilio*, including silvicultural practices such as reducing the density of trees, and introduction of biological control agents such as various species of hymenopteran parasitoids and the entomophagous nematode *Deladenus siricidicola* Bedding (Haugen et al. 1990, Bedding 2009). This nematode species was introduced from Europe, whereas the parasitoid species were introduced from both Europe and North America (Bedding 2009, Cameron 2012). These three integrated pest management (IPM) practices have considerably reduced the economic damage by *S. noctilio* in many countries in the southern hemisphere, especially in Australia and New Zealand (Cameron 2012).

Sirex noctilio has caused substantial economic damage to invaded areas in the southern hemisphere, but it is primarily colonizing weakened or suppressed trees in northeastern North America (Dodds et al. 2010). The major impacts of *S. noctilio* in North America may be in the western and southeastern regions of the United States where there are large tracts of suitable hosts and unthinned pine plantations (USDA Forest Service 2005). We hypothesize that North American forests may be better defended against colonization by *S. noctilio* than forests in southern hemisphere because of strong bottom-up and top-down population regulation factors. In the southern hemisphere, siricids have few natural enemies and competitors, whereas the North American forests have a rich complex of hymenopteran parasitoids, and bark and woodboring insect competitors (Wood 1982, Lingafelter 2006). This is especially true for the southern forest stands in the United States where there are seven species of native siricids (Schiff et al. 2006), and >50 species of bark (Coleoptera: Curculionidae: Scolytinae) and cerambycid beetles (Coleoptera: Cerambycidae) (Wood 1982, Lingafelter 2006). Some of these species, such as the southern pine beetle (*Dendroctonus frontalis* Zimmerman) and rhizophagous beetles (*Hylastes* spp.), have their own suite of fungal symbionts (e.g., *Ophiostoma* spp. and *Leptographium* spp.) thus, adding to the complexity of potential interactions with *S. noctilio* (Klepzig and Wilkens 1997, Eckhardt et al. 2004, Ryan et al. 2011).

Regional surveys on hymenopteran parasitoids in North America have been conducted primarily as an attempt to find effective biological control agents for *S. noctilio.* For example, Kirk (1974, 1975) collected parasitoids in the southern portions of the United States, whereas Cameron (1962, 1963, 1965, 2012) spent several years collecting parasitoids in eastern Canada and the western United States, especially in the burned areas in California. Several parasitoid species from North America have been released in the southern hemisphere with mixed results, and successful establishment occurred in at least three species

(Hurley et al. 2007, Collett and Elms 2009). Cameron (2012) recently synthesized the history of use of parasitoids as biological control agents for *S. noctilio* for the southern hemisphere. This excellent review includes information about which parasitoid species were selected and introduced, from which parts of the world, whether they became established in the non-native range, and their biocontrol impacts on *S. noctilio*. Although there is much known about these parasitoids in relation to usefulness as management of *S. noctilio* in the southern hemisphere, there is no literature synthesizing and reviewing the ecology and natural history of these insects in North America. Our objective is to synthesize the known ecological information about North American hymenopteran parasitoids of siricids, including their distribution, life cycle, seasonal phenology, impacts on their native siricid hosts, and potential role as a biological control agent for *S. noctilio*. Through this review, we will also assess major knowledge gaps and provide future directions for research on these biological control taxa. As *S. noctilio* continues to expand its distribution in North America, a better understanding about when, where, and how to sample parasitoids for enhancing biological control of the exotic woodwasp species may become more essential with time.

The Ecology of Hymenopteran Parasitoids of the Siricidae in North America. Hymenopteran parasitoids are well known, and in the case of siricid woodwasps, these parasitoids in North America are present in three families: Stephanidae, Ibaliidae, and Ichneumonidae (Smith et al. 2006). Within these families, 26 species and subspecies of hymenopteran parasitoids are present including one species of Stephanidae, one genus and seven species of Ibaliidae, and three genera and 13 species of Ichneumonidae.

In addition to high species diversity, parasitoids also show diversity in parasitism habits (Vinson 1976, Mills 1994, Heimpel and Collier 1996). Siricid parasitoids are only known to use hosts for developing larvae, and similar to other hymenopteran parasitoids (Hawkins et al. 1992), they can be categorized under two groups: idiobionts and koinobionts. Idiobionts are generally ectoparasitoids where females may sting the host to either kill or immobilize it. Eggs then are laid on the stung host, and the host does not develop any further. Koinobionts are generally endoparasitoids where the host eggs or first instar is parasitized. The host is allowed to develop until it is completely consumed and the life cycle of the parasitoid is completed. Further, cleptoparasitism also has been recorded among siricid parasitoids where oviposition will occur on siricid larvae after they have already been preyed upon by conspecifics or competitors.

In the following sections, we provide specific information about each of the 26 hymenopteran siricid parasitoid species and subspecies including their 1) current taxonomic status (although valid subspecies are known for some of the parasitoid species, some studies did not report the sub-species; in these instances we provide general information about the species); 2) distribution in North America north of Mex-

ico; 3) collection habitat(s); 4) life cycle; 5) siricid host(s) (although it was not possible to deduce the exact siricid host in some studies because a number of siricid species emerged from the same trees and logs); 6) natural history observations; and 7) knowledge gaps about the species' ecology. We have grouped the species reviewed here into those that parasitize Siricinae and Tremicinae hosts, with a focus on Siricinae parasitoids that may exert greater control on *S. noctilio*.

Hymenopteran Parasitoids of the Subfamily Siricinae

Genus *Schlettererius* Ashmead (Hymenoptera: Stephanidae: Schlettererinae). *Schlettererius cinctipes* (Cresson) (formerly *Stephanus cinctipes*) is the only North American species in this genus (Townes 1949) (Fig. 1a). *Schlettererius cinctipes* occurs from the southwestern United States north to British Columbia, Canada, and east to South Dakota (Table 1). This species also is present in Virginia and Kentucky (Table 1), with the eastern United States populations likely transported from the western United States via human activity (Johansen et al. 2010). *Schlettererius cinctipes* has been reared from or in close association with several coniferous species (Table 1). This species has been found in association with trees killed in wildfires in California (Cameron 1963, 2012), and has been collected from windthrown trees a year after the 1962 severe windthrow in northern California (Wickman 1965).

The life cycle of *S. cinctipes* was documented by Taylor (1967) in a laboratory setting on radiata pine (*P. radiata* D. Don) logs containing *S. noctilio* larvae. Adults mated frequently in cages, with females mating more than once. Adult females oviposited roughly 2–3 wk after emergence, and are believed to detect host vibrations in wood via sensory organs on their tibia and tarsi (Vilhelmsen et al. 2008). Adults can reach at least 3.4 cm into the wood with their ovipositor to locate siricid larvae, which are stung and paralyzed before oviposition. Eggs hatched in 10–14 d, with the larvae needing up to 7 wk to complete development. *Schlettererius cinctipes* is an idiobiont ectoparasitoid, as parasitoid larvae attach to the outside of host larvae initially and extract host fluids, and later consume all but heavily sclerotized portions of the host larva. Larvae of *S. cinctipes* can be distinguished from other parasitoids by the presence of small sclerotized spines on the abdomen, along with distinct mouthparts in each instar (Taylor 1967). Pupal duration is unknown. Adults apparently emerge by pushing through the outer layers of the bark and leaving jagged edges; these exit holes are different from those of siricids and other parasitoids that have clean exit holes (Taylor 1967). Adult *S. cinctipes* are estimated to live about 1 mo, and have been collected from May to September, with peak activity in July (Cameron 1963, Kirk 1975, Johansen et al. 2010). Loose aggregations of adults have been documented in areas where a high density of host siricid larvae was present (Meyer et al. 1978).
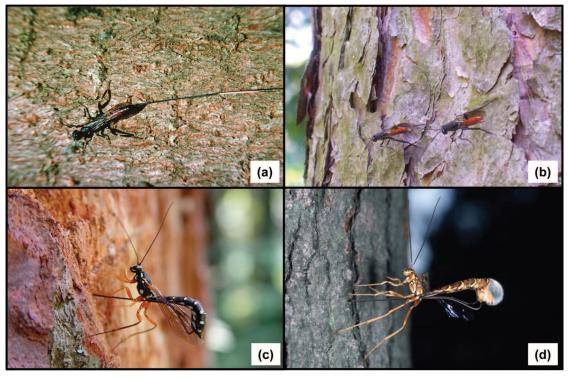
Fig. 1. Images of selected hymenopteran parasitoids of siricid wasps in North America north of Mexico: (a) *Schlettererius cinctipes* (Image Credit: Dennis Haugen, USDA Forest Service, Bugwood.org); (b) *Ibalia leucospoides* (Image Credit: Ethan Angell, NY State Department of Agriculture & Markets, Bugwood.org); (c) *Rhyssa* spp. (Image Credit: Boris Hrasovec, University of Zagreb, Bugwood.org); and (d) *Megarhyssa* spp. (Image Credit: Jim Occi, BugPics, Bugwood.org).

Purported siricid hosts for *S. cinctipes* include *Sirex*, *Urocerus*, and *Xeris* species (Table 1). Successful parasitism rates on *S. noctilio* of up to 32% were obtained in a laboratory (Taylor 1967), but field parasitism rates were <5% in Australia where it has been introduced (Collett and Elms 2009).

Additional research on the distribution and biology of *S. cinctipes* is needed, as basic life history questions such as natural host associations remain unknown. The efficacy of *S. cinctipes* as a biological control agent in North America is unknown, although research in the southern hemisphere suggests that this parasitoid may contribute, in part, to the management of *S. noctilio* (Taylor 1967, Collett and Elms 2009).

Genus *Ibalia* Latreille (Hymenoptera: Ibaliidae: Ibaliinae). *Ibalia* is the only genus in the family Ibaliidae, a group having a distribution worldwide in the northern hemisphere (Nordlander et al. 1996) (Fig. 1b). There are seven *Ibalia* species and subspecies native to North America (Liu and Nordlander 1992). All *Ibalia* species are endoparasitic koinobionts with up to a 3-yr life cycle, parasitizing eggs and first instars (Chrystal and Myers 1928, Chrystal 1930, Hanson 1939, Middlekauff 1960); however, the final instar is ectoparasitic. Females of *Ibalia* spp. oviposit on siricid larva by using the oviposition holes created by the female siricids (Spradberry 1970c, 1974). Only *I. anceps* Say parasitizes Siricidae on hardwoods; all other North American species in this genus parasitize Siricidae in conifer trees. *Ibalia* species respond to volatiles emitted by *Amylosterum* species, which are symbiotic fungi with woodwasps (Madden 1968, Spradberry 1974, Martínez et al. 2006). *Amylosterum areolatum* (Fr.) Boidin, symbiotic with *S. noctilio*, is considered one of the primary host location mechanisms for several parasitoid species (Spradberry 1970b,c; 1974).

Ibalia montana Cresson occurs throughout the western United States and Canada, and has been reared from several coniferous species (Table 1). Adults are active from late June to late July, with peak flight in early July (Kirk 1975). No further information about the life-cycle is known. Should *S. noctilio* populations reach western North America, this parasitoid may play a role in its management.

Ibalia rufipes rufipes (Cresson) was captured in the western United States, and uses siricid hosts in conifer trees (Table 1), although specific host associations are unknown. Adult flight occurs from mid-May to late June, peaking in early June, suggesting that newly hatched siricid larvae from overwintering eggs are the primary host (Kirk 1975). Although little is known regarding *I. r. rufipes* biology or behavior, this wasp is closely related to the European species *I. rufipes drewseni* Borries (Liu and Nordlander 1994). In a laboratory study using Scots pine (*Pinus sylvestris* L.), logs infested with *S. noctilio*, *Sirex juvencus* (L.), *Sirex cyaneus* (F.), *X. spectrum* (L.), or *Urocerus gigas* (L.)

Table 1. Locations, and host tree and siricid records, of the parasitoids of Siricidae found in North America

Hymenoptera family	Parasitoid species	State or province	Tree species record	Potential or actual siricid host	Reference
Stephanidae	*Schletterius cinctipes* (Cresson)	Washington Territory	*Pseudotsuga menziesii*		Cresson 1880 / Townes 1949
		Arizona, British Columbia, California, Idaho, Oregon, Washington			
		California	*Abies* spp. *Pinus jeffreyi*	*Xeris morrisoni*, *Xeris spectrum*	Cameron 1963
		Arizona, New Mexico	*Abies concolor, Pinus ponderosa*	*Sirex cyaneus, Sirex juvencus californicus, Sirex longicauda, Urocerus californicus, X. morrisoni morrisoni, X. spectrum*	Kirk 1975
		California	*A. concolor*		Meyer et al. 1978
		Virginia		*U. californicus, X. morrisoni, X. spectrum*	Smith 1997
		South Dakota	*Abies grandis, P. jeffreyi, Pinus lambertiana,*		Aguiar and Johnson 2003
Ibalidae	*Ibalia* spp.	Kentucky			Johansen et al. 2010
	Ibalia anceps Say	New Hampshire	*Abies balsamea*	*S. cyaneus*	Johnson 1930
		Arkansas			Say 1824
		Georgia			Westwood 1837
		Pennsylvania			Haldeman 1846
		Quebec	*Acer* spp., *Fagus* spp.	*Tremex columba*	Harrington 1889
		Pennsylvania	*Carya* spp.	*T. columba*	Champlain 1922
		Illinois			Weld 1922
		Texas			Weld 1952
		Colorado, Florida, Maryland, Massachusetts, Michigan, Missouri, New Jersey, New York, Nova Scotia, Ontario, Tennessee, West Virginia, Wisconsin			Liu and Nordlander 1994
	Ibalia montana Cresson	Virginia			Smith and Schiff 2002
		Colorado	*Picea glauca, P. menziesii*		Cresson 1889
		Montana, Oregon, Washington			Weld 1952
		British Columbia		*S. longicauda, U. californicus, X. morrisoni*	Cameron 1965
		New Mexico	*A. concolor*		Kirk 1975
	Ibalia rufipes rufipes (Cresson)	Arizona, California, Nevada		*S. longicauda, U. californicus, X. morrisoni*	Liu and Nordlander 1992
		Nevada			Cresson 1889
		Arizona, Colorado	*A. concolor, Abies lasiocarpa, P. ponderosa*	*S. cyaneus, S. juvencus californicus, S. longicauda, U. californicus, Urocerus gigas, X. spectrum*	Kirk 1975
	Ibalia kirki Liu and Nordlander	California, Oregon			Liu and Nordlander 1992
	Ibalia arizonica Liu and Nordlander	Arizona	*Pinus engelmanii*	*S. cyaneus, X. spectrum*	Liu and Nordlander 1992
		Arizona-New Mexico	Conifers	Siricidae	Liu and Nordlander 1992
	Ibalia ruficollis Cameron	Mexico			Cameron 1884
		Arizona	*P. ponderosa*	*S. juvencus californicus*	Kirk 1975
		Mexico			Liu and Nordlander 1994

Table 1. Continued

Hymenoptera family	Parasitoid species	State or province	Tree species record	Potential or actual siricid host	Reference
	Ibalia ensiger Norton	California	P. ponderosa	S. juvencus californicus	Cameron 1968
	Ibalia leucospoides (Hochworth)	Alberta, Arizona, California, Colorado, Florida, Georgia, Idaho, Maryland, Michigan, Minnesota, Mississippi, New Brunswick, North Carolina, Oregon, Pennsylvania, South Carolina, Utah, Virginia, Washington, West Virginia		Sirex, Urocerus, Xeris	Smith and Schiff 2002
		Ontario	Pinus banksiana, Pinus resinosa, Pinus sylvestris	Sirex nigricornis, Sirex noctilio	Ryan et al. 2012
	Ibalia leucospoides ensiger (Norton)	Pennsylvania	Tsuga spp.	Urocerus albicornis	Cresson 1865
		Pennsylvania	Cupressus macrocarpa	Sirex spp., Urocerus spp.	Champlain 1922
		California	P. ponderosa	Sirex areolatus, Sirex behrensii	Weld 1952
		California	A. concolor, Abies magnifica		Middlekauff 1960
			P. glauca	S. cyaneus, U. albicornis flavicornis	Cameron 1962
		Alberta, British Columbia, Manitoba, Ontario, Quebec			Yoshimoto 1970
		Alabama, Florida, Georgia, South Carolina	Pinus clausa, Pinus elliottii, Pinus palustris, Pinus taeda, Pinus virginiana	Sirex abbottii, S. nigricornis	Kirk 1974
		Arizona	P. engelmannii	S. cyaneus, X. spectrum	Kirk 1975
		British Columbia, Delaware, Idaho, Maine, Maryland, Michigan, Nevada, New York, North Carolina, Northwestern Territories, Nova Scotia, Ontario, Oregon, Quebec, Saskatchewan, Utah, Virginia, Washington, West Virginia			Liu and Nordlander 1992
		New York	P. sylvestris	Sirex eduardsii, S. nigricornis, S. noctilio	Long et al. 2009
		New York	P. resinosa, P. sylvestris	S. eduardsii, S. nigricornis, S. noctilio	Eager 2011
			Libocedrus decurrens	S. areolatus, X. spectrum	Cameron 2012
Ichneumonidae	Pseudorhyssa nigricornis (Ratzeburg)				Ratzeburg 1852
					Merrill 1915
		Ontario, Maine, Colorado, Washington Territory	Abies sp., A. concolor, Larix spp., Picea mariana, P. ponderosa	Siricidae	Townes and Townes 1960
		Alberta, Arizona, California, Colorado, Michigan, Maine, New York, Ontario, Quebec, Tennessee	Abies fraseri, Pinus rigida	S. abbottii, S. cyaneus, S. nigricornis	Kirk 1974
		North Carolina	A. concolor, A. lasiocarpa, P. englemannii	S. cyaneus, U. californicus, X. morrisii, X. spectrum	Kirk 1975
		Arizona			Porter 2001
	Rhyssa hoferi Rohwer	Maryland		S. eduardsii, S. nigricornis, S. noctilio	Standley et al. 2012
		New York	P. resinosa, P. sylvestris		Rowher 1920
		Colorado			Townes and Townes 1960
	Rhyssa ponderosae Townes	Arizona, Colorado	Juniperus spp., Pinus edulis		Kirk 1975
		Arizona	P. ponderosa	S. juvencus californicus, X. spectrum	Townes and Townes 1960
		California	P. ponderosa	S. areolatus	Cameron 1965
		California			

Table 1. Continued

Hymenoptera family	Parasitoid species	State or province	Tree species record	Potential or actual siricid host	Reference
	Rhyssa alaskensis Ashmead	Alaska			Ashmead 1902
		Alberta, British Columbia, California, Idaho, Montana, New Mexico, Oregon, Washington, Wyoming	*A. lasiocarpa, Picea sitchensis, Pinus contorta murrayana,*		Townes and Townes 1960
		Washington			Deyrup 1975
		Arizona	*P. menziesii*		Kirk 1975
	Rhyssa houdenorum (Townes and Townes)	Virginia, Nebraska, North Carolina	*P. virginiana*	*S. abbottii, S. nigricornis*	Townes and Townes 1960
		Alabama, Georgia, Maryland, South Carolina	*Pinus echinata, P. elliotti, P. palustris, P. rigida, P. taeda, P. virginiana*		Kirk 1974
		Florida, Oklahoma		*S. edwardsii, S. nigricornis, Urocerus cressoni*	Porter 2001
	Rhyssa crevieri (Provancher)	Ontario			Provancher 1880
		Maine, Minnesota, New Brunswick, New Hampshire, New Jersey, New York, North Carolina, Nova Scotia, Ontario	*A. balsamea*	*U. albicornis*	Townes and Townes 1960
		New York	*P. resinosa, P. sylvestris*	*S. edwardsii, S. nigricornis, S. noctilio*	Standley et al. 2012 Linnaeus 1758 Provancher 1880
	Rhyssa persuasoria (L.)	Canada			Townes and Townes 1960
		Alberta, British Columbia, Arizona, California, Colorado, Idaho, Manitoba, Massachusetts, Michigan, Minnesota, New Brunswick, New Hampshire, New York, North Carolina, Oregon, Ontario, Quebec, Tennessee, Texas, Utah, Vermont, Washington, Wyoming	*A. balsamea, A. concolor, P. edulis, P. menziesii, P. ponderosa, P. p. scopulorum*	*S. areolatus*	
		North Carolina	*A. fraseri, P. rigida*	*S. abbottii, S. cyaneus, S. nigricornis*	Kirk 1974
		Washington	*P. menziesii*		Deyrup 1975
		Arizona, Colorado	*A. concolor, A. lasiocarpa, P. engelmannii, P. ponderosa*	*S. cyaneus, S. juvencus californicus, S. longicauda, U. californicus, U. gigas, X. morrisoni, X. spectrum*	Kirk 1975
		New York	*P. resinosa, P. sylvestris*	*S edwardsii, S. nigricornis, S. noctilio*	Eager 2011
		Ontario	*P. banksiana, P. sylvestris*	*S. nigricornis, S. noctilio*	Ryan et al. 2012
		Canada			Kirby 1837
		Pennsylvania	Hemlock	*U. albicornis*	Champlain 1922
	Rhyssa lineolata (Kirby)	Alberta, British Columbia, Colorado, Connecticut, District of Columbia, Idaho, Maine, Massachusetts, Michigan, Minnesota, New Hampshire, New York, North Carolina, Nova Scotia, Ohio, Ontario, Quebec, South Carolina, Vermont, Virginia, Washington, West Virginia	*A. balsamea, A. lasiocarpa, Picea* spp., *P. sitchensis, Tsuga canadensis*		Townes and Townes 1960
		North Carolina	*A. fraseri, P. rigida*	*S. abbottii, S. cyaneus, S. nigricornis*	Kirk 1974
		Washington	*P. menziesii*		Deyrup 1975
		New York	*P. sylvestris*	*S. edwardsii, S. nigricornis, S. noctilio*	Long et al. 2009
		New York	*P. resinosa, P. sylvestris*	*S. edwardsii, S. nigricornis, S. noctilio*	Eager 2011
		Ontario	*P. banksiana, P. sylvestris*	*S. nigricornis, S. noctilio*	Ryan et al. 2012

Table 1. Continued

Hymenoptera family	Parasitoid species	State or province	Tree species record	Potential or actual siricid host	Reference
	Megarhyssa nortoni (Cresson)	Pennsylvania		*U. albicornis*	Champlain 1922 Michener 1939
		British Columbia, California, New York, Oregon, Washington			
		New York	*P. sylvestris*	*S. eduardsii, S. nigricornis, S. noctilio*	Long et al. 2009
		California		*S. areolatus, S. juvencus californicus, S. longicauda*	Cameron 2012
	Megarhyssa nortoni nortoni (Cresson)	Colorado			Cresson 1864
		California		*X. morrisoni*	Middlekauff 1960
		Alaska, Alberta, Arizona, British Columbia, California, Colorado, Idaho, Michigan, Montana, Oregon, Ontario, Utah, Vermont, Washington	*A. concolor, A. grandis, A. lasiocarpa, A. magnifica, P. contorta murrayama, P. jeffreyi, P. menziesii, P. sitchensis, P. ponderosa, cedar*		Townes and Townes 1960
		California	*P. jeffreyi*	*S. juvencus californicus*	Cameron 1967
		Washington	*P. menziesii*		Deyrup 1975
		Arizona	*A. concolor, P. englemannii, P. ponderosa*	*S. cyaneus, S. juvencus, S. longicauda. U. albicornis, X. spectrum*	Kirk 1975
	Megarhyssa nortoni quebecensis (Prov.)	Quebec	*T. canadensis*	Siricidae	Provancher 1873
		Connecticut, Michigan, Minnesota, New Brunswick, Newfoundland, New Hampshire, New York, North Carolina, Nova Scotia, Ontario, Quebec, Pennsylvania, Prince Edward Island, Tennessee, Vermont			Townes and Townes 1960
	Megarhyssa atrata (F.)	Georgia	*Fagus* spp.	*T. columba*	Fattig 1949
	Megarhyssa atrata atrata F.	North America	*Carya* spp, *Fagus* spp.	*T. columba*	Fabricius 1781
		Arkansas, Connecticut, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Ontario, Pennsylvania, South Dakota, Tennessee, Vermont, Virginia, West Virginia, Wisconsin, Wyoming			Townes and Townes 1960
	Megarhyssa atrata lineata Porter	New Hampshire	*Acer rubrum*	*T. columba*	Porter 1957
		Maine, Michigan, New Brunswick, New Hampshire, Nova Scotia, New York, Ontario, Pennsylvania, Quebec, Vermont, Wisconsin			Townes and Townes 1960
	Megarhyssa lunator lunator (F.)	New York			Michener 1939
	Megarhyssa lunator phaeoptila Michener	Louisiana, Texas	*Quercus* spp.		Michener 1939
	Megarhyssa macrurus (L.)	Georgia	*Fagus* spp.	*T. columba*	Fattig 1949

Table 1. Continued

Hymenoptera family	Parasitoid species	State or province	Tree species record	Potential or actual siricid host	Reference
	Megarhyssa macrurus macrurus (L.)	South Carolina			Linnaeus 1771
		Florida, Georgia, Louisiana, Mexico, Texas			Townes and Townes 1960
	Megarhyssa macrurus icterosticta Michener	Colorado, New Mexico, Utah			Michener 1939
		Arizona, New Mexico, Utah			Townes and Townes 1960
	Megarhyssa macrurus lunator (F.)	North America			Fabricius 1781
		Illinois	Acer saccharinum, Ulmus spp.	T. columba	Abbott 1934
		Alabama, Connecticut, Colorado, Delaware, District of Columbia, Georgia, Illinois, Indiana, Iowa, Kansas, Louisiana, Maine, Massachusetts, Michigan, Minnesota, Missouri, Nebraska, New Jersey, New Mexico, New York, North Carolina, Ohio, Ontario, Pennsylvania, Quebec, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin	Acer spp., Acer negundo, A. rubrum, Carya sp., Celtis spp., Fagus spp., Quercus alba, Ulmus spp.	T. columba	Townes and Townes 1960
	Megarhyssa greenei Viereck	Georgia	Fagus spp.	T. columba	Fattig 1949
	Megarhyssa greenei greenei Viereck	New York			Michener 1939
	Megarhyssa greenei greenei Viereck	Connecticut, Indiana, Michigan, New Jersey, Pennsylvania	Acer spp.		Viereck 1911
		Alabama, Connecticut, Delaware, District of Columbia, Georgia, Illinois, Indiana, Iowa, Kansas, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New York, North Carolina, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, South Carolina, Tennessee, Vermont, Virginia, West Virginia, Wisconsin	Acer rubrum, Carya spp., Fagus spp, Q. alba	T. columba	Townes and Townes 1960
	Megarhyssa greenei floridana Townes	Florida			Townes and Townes 1960

Host tree records indicate tree species from where parasitoid adults emerged or larvae were collected. Siricid hosts are either actual or potential (i.e., parasitoids and adult siricids emerged from the same host material) hosts.

were offered to females of *I. r. drewseni* (Spradberry 1970c). Adults emerged from mid-May to mid-June, mated readily in captivity, and produced 175 eggs per female. Adults can reach their ovipositor over 8 mm deep in wood to deposit an egg on a host larva, generally depositing one (but up to three) eggs per larva. Parasitoid larval development is complete in 50 d, pupation takes up to 20 d, with adults emerging on average 104 d after oviposition. Adult *I. r. drewseni* can live over 1 mo. Because of *I. r. drewseni*'s early emergence compared with its siricid hosts, this parasitoid plays a relatively small role as a biological control agent, but does fill a niche in attacking eggs with advanced embryos or first through third-instar siricids (Spradberry 1970c, Taylor 1976). Assuming similar biology to *I. r. drewseni*, it is possible that *I. r. rufipes* may play a role in *S. noctilio* management in western North America.

Ibalia kirki Liu and Nordlander and *Ibalia arizonica* Liu and Nordlander, two species reared from pine and spruce logs containing siricid larvae (Kirk 1975), were once thought to be *Ibalia leucospoides* (Kerrich 1973) until a re-examination of the material (Liu and Nordlander 1992). These two species, and *Ibalia ruficollis* Cameron, occur in the southwestern United States and Mexico (Table 1). Adults emerged from coniferous species, and are believed to be hosts on *Sirex* and *Xeris* spp. (Table 1), although no further information is known. Should *S. noctilio* invade the southwestern United States, *I. kirki*, *I. arizonica*, and *I. ruficollis* may play a role in *S. noctilio* management.

Ibalia leucospoides ensiger (Norton) (formerly *I. leucospoides*) is possibly the most well-known and common biological control agent for *S. noctilio*. Unfortunately, this species is sometimes confused with *I. leucospoides leucospoides* (Hochenwarth) (formerly *I. leucospoides*). *Ibalia l. ensiger* is Nearctic species with a yellowish brown metasoma, whereas *I. l. leucospoides* species is Palearctic and has a darker metasoma (Liu and Nordlander 1994). Although some taxonomists do not recognize subspecies of *I. leucospoides* (Smith and Schiff 2002), we recognize the two *I. leucospoides* subspecies for purposes of this review. *Ibalia l. ensiger* occurs across much of North America (Table 1). *Ibalia l. ensiger* is present from late April through mid-November in the mid-Atlantic States (Smith and Schiff 2002), likely with a shorter flight period north of this area. *Ibalia l. ensiger* has emerged from many coniferous species, and uses larval siricids from the genera *Sirex*, *Urocerus*, and *Xeris* as hosts (Table 1). This species also has been reared in high numbers from trees burned in wildfires in California (Cameron 1963). Immature stages were dissected from logs of white fir [*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.] and California red fir (*Abies magnifica* A. Murr.) in California (all failed to develop to adult stage, perhaps because of removal from logs) (Cameron 1962). It has been collected on windthrown trees a year after the 1962 severe windthrow in northern California (Wickman 1965). *Ibalia l. leucospoides* (Hochenwarth) is one of the most successful parasitoids for *S. noctilio* control in Australia, as it easily has

established (Taylor 1976) and parasitizes nearly 20% of the *S. noctilio* population in Tasmania (Taylor 1978) and nearly 60% of the *S. noctilio* population in Victoria (95% of parasitoid activity is *I. leucospoides* or *I. l. leucospoides* × *I. l. ensiger* hybrids) (Collett and Elms 2009). Female *I. l. leucospoides* are solitary, but unaffected by conspecifics—only prey abundance affects foraging effort (Corley et al. 2010). However, larger females do have some competitive advantages in that they can outcompete smaller females for oviposition sites (Fernandez-Arhex and Corley 2010) and fly longer distances in search of prey (Fischbein et al. 2011). In North America, *I. l. ensiger* has potential to be an integral part of a natural enemy complex for *S. noctilio*, as this parasitoid accounted for over 78% of total parasitism in Scots and red (*P. resinosa* Ait.) pine with *S. noctilio*, *S. nigricornis*, and *S. edwardsii* Brullé as prey (Long et al. 2009, Eager et al. 2012). Further, *I. l. ensiger* has been reared from logs infested with native siricids in 2009–2011 in Louisiana with varied parasitism rates of 6–44% as depending upon site and year (J. Meeker and W. Johnson, personal communication). The antennae of *I. l. ensiger* have been found to respond to compounds isolated from *A. areolatum*, although no adults were caught when these compounds were field-tested in the forests of New York (Bryant 2011).

Parasitoids in the genus *Ibalia* have potential to impact *S. noctilio* populations in North America. Although little is known regarding *I. anceps*, *I. montana*, *I. rufipes rufipes*, *I. arizonica*, *I. kirki*, and *I. ruficollis*, much more is known about the ecology of *I. l. ensiger*. Future research focusing on the lesser known *Ibalia* species would be beneficial to determine how these species might fit into an IPM plan for *S. noctilio* at a regional level. Research on *I. l. ensiger* is still in its infancy in North America, and much more remains to be discovered regarding host specificity and impacts of this species on *S. noctilio* populations.

Genus *Pseudorhyssa* (Merrill) (Hymenoptera: Ichneumonidae: Poemeniinae). The genus *Pseudorhyssa* contains three species worldwide, of which only one occurs in North America (Kusigemati 1984, Yu and Horstmann 1997). *Pseudorhyssa nigricornis* (Ratzeburg) has been captured in eastern Canada and the northeastern United States, south to North Carolina, and also west of the Rocky Mountains (Table 1). *Pseudorhyssa nigricornis* is an idiobiont cleptoparasite on several *Rhyssa* species, including *R. howendorum* (Townes); *R. persuasoria* (L.); *R. lineolata* (Kirby) (Spradbery 1968a,b; Kirk 1974); and possibly *Megarhyssa nortoni* (Cresson) (Standley et al. 2012), and often is associated with coniferous woody hosts (Table 1).

Adult populations peak in numbers in May and June (Spradbery and Kirk 1978), but with the exception of Spradbery (1968b) little is known regarding the biology of *P. nigricornis*. Adult females can live nearly 6 wk, and use extracts from *Rhyssa* vaginal glands as attractants. Female *P. nigricornis* generally observe as *Rhyssa* females oviposit, insert their ovipositor into the hole drilled by the rhyssine, and oviposit near the egg

left by the primary parasite. After a 48-h incubation period, the *P. nigricornis* egg hatches, and the larva finds, attacks, and kills the *Rhyssa* larva, consuming portions of its victim in the process. *Pseudorhyssa nigricornis* larvae are fierce fighters, killing *Rhyssa* larvae of all ages, and even fighting to the death in the case of superparasitism. The *P. nigricornis* larva then pierces the host cuticle, and begins to consume its body fluids. All but the host cuticle and head capsule are consumed by the *P. nigricornis* larva within a period of 2 wk. The larva spins a cocoon inside the host chamber, overwinters, and pupates in the spring. *Pseudorhyssa nigricornis* can be a moderate component of siricid control in some European countries (Spradbery and Kirk 1978), although it is eliminating another biological control agent (*Rhyssa* spp.) during this process.

Very little is known regarding this cleptoparasitoid other than its biology in the laboratory. Standley et al. (2012) reported 26% cleptoparasitism of rhyssines in New York, with *P. nigricornis* emergence peaking in May and early June along with *R. persuasoria, R. lineolata,* and *M. nortoni* populations. Research is needed to determine the effect of cleptoparasitism by *P. nigricornis* on *Rhyssa* spp., and how these interactions may affect population dynamics of both parasitoids and siricid hosts in North America.

Genus *Rhyssa* Gravenhorst (Hymenoptera: Ichneumonidae: Rhyssinae). Parasitoids in the genus *Rhyssa* are large (body up to 4 cm in length) idiobiont ectoparasitoids of late-instar Siricidae (Fig. 1c). *Rhyssa* spp. have been reported to emerge from logs infested with *X. macgillivrayi* Bradley and *X. spectrum* in California (Cameron 2012). *Rhyssa* spp. are univoltine, overwintering in the larval stage and pupating in the spring (Middlekauff 1960). Certain species of *Rhyssa* have shown real or potential biological control abilities for *S. noctilio.*

Rhyssa hoferi Rohwer occurs in the southwestern United States and is parasitic on *Xeris* and *Sirex* spp. infesting conifer trees (Table 1). Adults fly from June to August (Townes and Townes 1960, Porter 2001). *Rhyssa hoferi* were imported to Tasmania and Victoria, Australia as a biological control agent for *S. noctilio,* and over 1,600 individuals were released between 1971 and 1985 (Taylor 1976, Collett and Elms 2009), and by 1988 had established populations in Australia (Haugen and Underdown 1990). Kirk (1975) observed this parasitoid using *Xeris* spp. and *Sirex* spp. as hosts in Arizona, and this parasitoid may play a role in biological control of *S. noctilio* should it invade the southwestern United States.

Rhyssa ponderosae Townes is known only from central California (Table 1). Adults were collected from April to June (Townes and Townes 1960). This species parasitizes *Sirex* larvae in ponderosa pine (Table 1). Nothing more is known regarding this species' biology or ecology.

Rhyssa alaskensis Ashmead occurs in western North America (Table 1). This species has been reared from several coniferous tree species (Table 1) and from wildfire-burned trees in California (Cameron 2012).

Adults have been collected from late May through early September (Townes and Townes 1960). Specific siricid hosts are unknown, as is much of this insect's biology and ecology.

Rhyssa howdenorum (Townes) is found throughout the southeastern United States (Table 1). This species has been collected from several pine species, and uses siricid species in the genera *Sirex* and *Urocerus* as hosts (Table 1). Adults are present from late April through late July, with the majority of adult emergence occurring in June (Townes and Townes 1960, Porter 2001); however, emergence can occur in early March, and possibly February in Louisiana (J. Meeker and W. Johnson, personal communication). Little is known about this parasitoid's biology, but it may play a role in *S. noctilio*'s biological control should the host become available.

Rhyssa crevieri (Provancher) is an uncommon species in the northeastern United States and Canada parasitizing *U. albicornis* in *Abies balsamea* (L.) Mill. (Table 1). Most adults are present in June, although several specimens have been taken in late-August (Townes and Townes 1960). We know very little regarding this parasitoid's biology, ecology, or biological control potential.

Rhyssa persuasoria (L.) is found in the eastern and western regions of North America (Table 1). Adults are found throughout the summer, and as late as October (Townes and Townes 1960). *Sirex, Urocerus,* and *Xeris* spp. larvae are parasitized in coniferous trees (Table 1). Adults of *R. persuasoria* lived up to 75 d and laid 15 eggs in captivity, and the life-span of individuals that were fed carbohydrates increased by 4–5 times, and starved females laid significantly fewer eggs than fed ones (Hocking 1967). Females of *R. persuasoria* are known to show aggressive behavior when they encounter one another while drilling or surveying the bark (Spradbery 1970a). *Rhyssa persuasoria* oviposit to depth >5 cm primarily through fissures and cracks in bark and wood (Spradbery 1968a, 1970a). Drills made by females are not random, rather concentrated along siricid galleries, and females can detect and parasitize dead siricids indicating that chewing sounds of siricids may not be necessary for finding them (Spradbery 1970a). Frass created by siricid larva and 3–4-mo-old fungal symbionts were the most attractive to *R. peruasoria* (Spradbery 1970a). Females will readily oviposit in captivity (Spradbery 1968a), making them an excellent candidate for mass rearing as a biological control portion of an IPM plan for *S. noctilio.* Extensive host finding observations were conducted in a laboratory where 23% parasitism of siricids occurred (Spradbery 1970a). While *R. persuasoria* represents a small portion of *S. noctilio* parasitism in North America (Eager 2011), up to 31% parasitism has been recorded on *S. noctilio* in other regions of the world (Morgan and Stewart 1966, Collett and Elms 2009). There is some evidence that *R. persuasoria* may compete with *Megarhyssa nortoni nortoni* Cresson in introduced areas such as Australia, as they both have repellents (such as 6-methylhept-5-en-2-one) for interspecies competition, and attractants for their own species

such as 3-hydroxy-3-methylbutan-2-one that are released from the adult mandibular glands (Davies and Madden 1985).

Rhyssa lineolata (Kirby) is found throughout eastern North America, and in the northern regions of western North America (Table 1). This relatively common parasitoid attacks siricids from the genera *Sirex* and *Urocerus* on many coniferous species (Table 1). Adults are present from May to October (Townes and Townes 1960). *Rhyssa lineolata* has been documented as a minor portion of the parasitoid complex for *S. noctilio* in North America (Long et al. 2009, Eager et al. 2011). Thus, *R. lineolata* could be a component of a natural *S. noctilio* biological control program in North America. *Rhyssa lineolata* was introduced to New Zealand unintentionally (Zondag and Nuttal 1961). There is some evidence that *R. lineolata* may have hyperparasitized *R. persuasoria* in New Zealand, where after >30 yr of established *R. persuasoria* populations, a greater proportion of *R. lineolata* rather than *R. persuasoria* emerged from logs (Zondag and Nuttal 1961).

Genus *Megarhyssa* Ashmead (Hymenoptera: Ichneumonidae: Rhyssinae). This genus contains some of the largest and most visually dynamic parasitoids of Siricidae, of which four species occur in North America (Fig. 1d). These parasitoids are ectoparasitic idiobionts on late-instar siricids (Middlekauff 1960). *Megarhyssa* spp. have a haplodiploid system where females are produced from fertilized eggs (Nuttall 1973a).

Megarhyssa nortoni occurs throughout much of North America, from the northeastern to the southwestern United States (Table 1). The species is divided into two subspecies, *M. n. nortoni* and *M. nortoni quebecensis* Provancher. *Megarhyssa n. nortoni* occurs primarily in western North America, whereas *M. n. quebecensis* has a predominantly eastern distribution (Table 1). Both subspecies attack Siricidae larvae from the genera *Sirex* and *Urocerus* in coniferous tree hosts (Table 1). In California, *M. nortoni* (no subspecies identified, but locality suggests *M. nortoni nortoni*) has been reared from wildfire-burned trees (Cameron 2012) and collected from windthrown trees a year after the windstorm (Wickman 1965). *Megarhyssa nortoni* has been collected from trees where *X. morrisoni* (Cresson) had been observed ovipositing (Middlekauff 1960).

Adults are active in June and August (Townes and Townes 1960, Kirk 1975). Males seemed to fly up to 3.7–4.6 m, whereas females were flying at the height of 4.6–9.1 m with a preference for open and sunny areas in California (Cameron 1963). Males use female mandibular secretions as attractants (Matthews et al. 1979, Davies and Madden 1985), which can lead to male aggregations at female emergence sites. The mandibular secretions contained interspecific attractants such as various alkyl spiroacetals, and also repellent compounds for other parasitoids (Davies and Madden 1985). Males have been known to mate with females that either have or have not yet emerged (Nuttall 1973a, b). Males insert their abdomen in the newly made exit hole of females and remain there for 15–19 min, after which females emerge from the wood (Nuttall 1973b). After mating, the females drill a hole 70 mm deep in wood to lay eggs on siricids (Tribe and Cillié 2004). The developing larvae are ectoparasitic, and they feed on late instar and pupal stages of *S. noctilio*, and presumably do the same on their native hosts (Neumann and Morey 1984). *Megarhyssa* spp. overwinter in the larval stage, and pupation takes places in the spring; life-cycle is 1-yr long (Middlekauff 1960). *Megarhyssa n. nortoni* accounts for only a small portion of *S. noctilio* parasitism in areas where it has been introduced (Taylor 1976, Neumann and Morey 1984) and where it naturally occurs in the Great Lakes region of North America (Eager 2009, Long et al. 2009).

Hymenopteran Parasitoids of the Subfamily Tremicinae

Genus *Ibalia*. *Ibalia anceps* is found across much of the eastern United States west to Colorado, and as far north as Ontario and New Brunswick, Canada (Table 1). Adults fly from late April through mid-July, with isolated collections in September (Smith and Schiff 2002). *Ibalia anceps* has not been reported parasitizing *Sirex* spp. (Table 1). Smith and Schiff (2002) reported that *I. anceps* likely parasitizes young *Tremex columba* L. larvae. Adults appear to reuse oviposition holes previously created by their siricid hosts (Weld 1922).

Genus *Megarhyssa*. *Megarhyssa atrata* (F.), *Megarhyssa macrurus* (L.), and *Megarhyssa greenei* Viereck all have similar life histories, and all are parasitoids on *T. columba* (Middlekauff 1960, Stillwell 1967). These three species occur in the northeastern United States west to Michigan, and in southern Canada (Townes and Townes 1960, Heatwole et al. 1964). *Megarhyssa atrata* flies from May to September in southern Quebec, Canada, and can represent up to 50% of the *M. atrata*, *M. macrurus*, and *M. greenei* population complex (Nénon 1995), however, the majority of activity is on hardwoods during June and July (Heatwole and Davis 1965). These three sympatric species each target larvae at different depths in the wood, as evidenced by the different lengths of their ovipositors—*M. greenei* (approximate range of ovipositor length is 30–60 mm) attack siricid larvae closest to the bark, *M. macrurus* (55–100 mm) attack larvae deeper than *M. greenei* (100–140 mm) but shallower than *M. atrata*, whereas *M. atrata* can drill up to 14 cm into wood to locate a host (Heatwole and Davis 1965). In the beech (*Fagus* spp.) forests of Michigan, *M. greenei*, *M. macrurus*, and *M. atrata* were respectively associated with the youngest, moderate, and oldest wood decay class (Heatwole and Davis 1965, Gibbons 1979). Adults live up to 4 wk (Heatwole and Davis 1965), and generally rest on the undersides of leaves, as noted on beech and maple (*Acer* spp.) trees (Heatwole and Davis 1965). To our knowledge, only one study (Heatwole and Davis 1965) has examined siricid larval parasitism by this complex of *Megarhyssa* species, and they found over
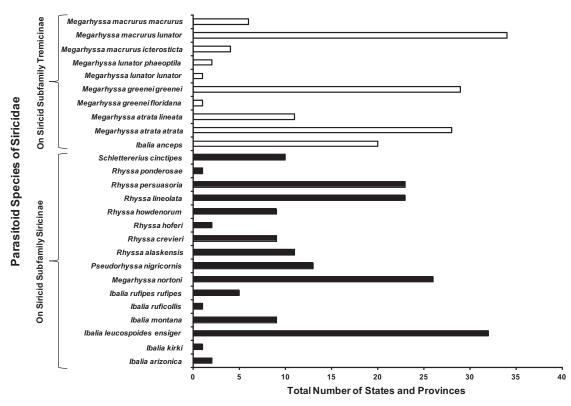
Fig. 2. Geographic distribution of the hymenopteran parasitoids of Siricidae in subfamilies Siricinae and Tremicinae documented from United States and Canada. Note that *Megarhyssa nortoni nortoni* and *M. nortoni quebecensis* are placed together as *M. nortoni*.

26% of *T. columba* larvae were parasitized by this species.

Males show interesting mixed-species aggregation behavior on trees from which they emerged from with high site fidelity (Matthews et al. 1979, Crankshaw and Matthews 1981). On beech trees in New York, males interacted with each other by lashing of antennae, wing vibrations, flexing of abdomen, and butting of heads (Matthews et al. 1979). In addition, they showed a distinctive behavior termed "tergal stroking" in which they stroked the tree's surface by pushing the abdomen anteriorly through the legs with tergum touching the bark, and moving side-to-side. An anal sac was found on the last abdominal segment, and it's possible that the males were putting odors on the bark. Males also inserted their abdomen through bark crevices and emergence holes (Matthews et al. 1979). Both postemergence and preemergence mating has been observed in various *Megarhyssa* species, with males perhaps cuing on chewing sounds and other olfactory cues by females (Heatwole et al. 1963, 1964; Crankshaw and Matthews 1981). Mixed-species male aggregations often form on logs where females are about to emerge (Matthews et al. 1979), and they copulate either after female emergence, or before female emergence by inserting the abdomen into the emergence hole of the female (Crankshaw and Matthews 1981).

Although *M. atrata*, *M. macrurus*, and *M. greenei* can be abundant in some forests, their potential to be used as a biological control for *S. noctilio* is small, as they oviposit on siricid larvae present in hardwoods instead of coniferous trees.

Little is known regarding the ecology of *Megarhyssa macrurus lunator* (F.) except for one study that reported larvae moving close to the log surface before pupating (Abbott 1934). Females appear to mate only once with mating lasting a few seconds. The average diameter of the exit holes of females was larger (4.3 mm) than males (2.3 mm). The biological control potential of this parasitoid species is unknown.

Summary. Overall, a species-rich community of hymenopteran parasitoids is associated with diverse native siricids and tree hosts in North American forest stands. Similar to parasitoids of other taxonomic groups, these species appear to be highly coevolved with their host(s), and as a group, are widespread across the continent and present in many forest-types. The three major trends from this review of the ecology of 26 species and subspecies of hymenopteran parasitoids of siricids in North America are as follows:

1) Geographic Distribution. Hymenopteran parasitoids are widely distributed in North American forests, and have been reported from many forest-types (Table 1). Overall, *M. m. lunator* was reported from
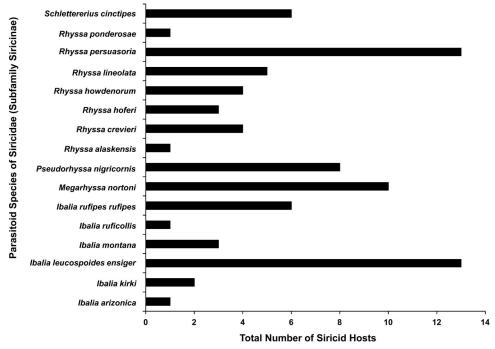
Fig. 3. Total number of hymenopteran parasitoid species associated with their Siricinae siricid host species (only conifer trees) in North America.

the greatest number of states and provinces (34) followed by *I. l. ensiger* (32), *M. g. greenei* (29), and *M. a. atrata* (28) (Fig. 2). These *Megarhyssa* species may be widely distributed, but they may have been more easily observed and identified because they are large, colorful, and exhibit aggregation behavior. Among parasitoids using Siricinae as hosts, *I. l. ensiger* (32) was most widely distributed in North America followed by *M. nortoni* (26), *R. persuasoria* (23), and *R. lineolata* (23). Cameron (2012) suggested that the effects of the presence of multiple species of parasitoids may be additive and not competitive in their introduced range. There may be competitive exclusion as based on climatic conditions. For example, in their nonnative range, *Megarhyssa* spp. were the most important parasitoids in cooler and more temperate climates, whereas *Rhyssa* spp. and *Ibalia* spp. were more important in warmer and arid climates (Cameron 2012). Further, populations of *M. nortoni* and *R. persuasoria* appear to be affected by delayed density-dependent factors, while *I. leucospoides* populations may be affected by density independent factors in controlling *S. noctilio* in Tasmania (Taylor 1978).

2) Host Range on Siricids. Hymenopteran parasitoids were associated with a total of 16 native and one exotic (*S. noctilio*) siricid species (Table 1). In the subfamily Siricinae, *R. persuasoria* and *I. l. ensiger* parasitized the greatest number of siricid species (13), followed by *M. nortoni* (11), and *P. nigricornis* (8) (Fig. 3). Only *T. columba* and *E. formosanus* have been reported to use hardwood trees as hosts. Hymenopteran parasitoids of the siricid subfamily Tremicinae

were unique from those of Siricinae, and there appears to be no cross-over of parasitoids across these two subfamilies (Table 1) (Cameron 2012). Hence, only hymenopteran parasitoids of the native siricid subfamily Siricinae, whose larvae are present in conifer trees, may have any effect on *S. noctilio* populations.

3) Host Range on Trees. Parasitoids were associated with a total of 110 tree species including 90 conifer and 20 hardwood trees (Table 1). Within conifer tree species, *I. l. ensiger* was associated with the greatest number of trees (16), followed by *R. persuasoria* (14), *M. nortoni* (14) and *R. lineolata* (10) (Fig. 4). Our synthesis indicates that *I. l. ensiger, R. persuasoria, R. lineolata,* and *M. nortoni* are the most widely distributed throughout North America, and with the widest host range on siricid wasps and conifer trees, and may have the greatest impact on *S. noctilio* populations. Both *S. cinctipes* and *P. nigricornis* may exert an additional control on *S. noctilio*. Interactions of these species with *S. noctilio* are likely going to be dependent upon the geographic location and local climatic conditions. At present, most of the information about *S. noctilio* and native parasitoids is known from the New York (Eager 2009, Long et al. 2009, Eager et al. 2011, Standley et al. 2012) and Ontario, Canada forests (Ryan et al. 2012). It remains to be seen if parasitism rates increase or decrease over time, and whether other native parasitoid species may start showing associations with *S. noctilio*.

Our literature review revealed five major knowledge gaps in the ecology and behavior of siricid parasitoids of subfamily Siricinae in North America. Firstly,
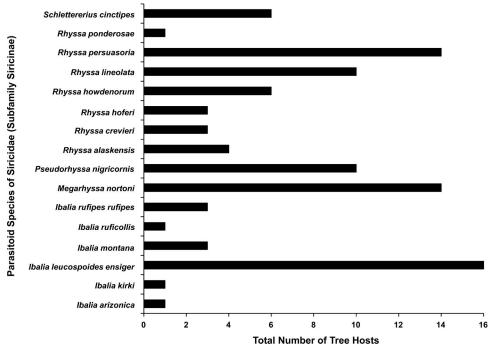
Fig. 4. Total number of hymenopteran parasitoid species on siricid subfamily Siricinae associated with their tree hosts (only conifer trees) in North America.

there appears to be taxonomic uncertainty about several species, especially their subspecies (e.g., the *I. leucopoides* and *M. nortoni* group). Some genera may need revision as more collections are made across the continent in the future. Secondly, full distribution ranges of many North American hymenopteran parasitoids are unknown, especially from the southwestern United States and northern Canadian forests (e.g., those of *R. hoferi* and *R. pondersoae*). A full distribution range of parasitoids may require both field sampling and accessing records of deposited specimens at major museums in the United States and Canada. Thirdly, although there are records of siricid and tree hosts associated with each of these parasitoids, a major knowledge gap still exists in exactly matching each parasitoid species to its host(s). In many instances, hosts are listed as only siricid wasps (e.g., for *I. arizonica*) and tree genera (e.g., for *P. nigricornis*), and are reared from logs from which multiple siricid hosts also emerged (e.g., for *I. l. ensiger*). Rearing studies from various tree species and siricid species, and/or DNA barcoding of larval parasitoids and siricids may be required to match parasitoid to host. In fact, an effective DNA barcoding method for siricid larvae has already been developed (Wilson and Schiff 2010), which may be modified to work on parasitoids. Fourthly, we do not know how *S. noctilio* populations may affect native parasitoid and siricid populations. If there is a positive feedback to parasitoids, then we would expect that native siricid species (especially in the subfamily Siricinae) may be negatively affected by increased parasitism, other than through possible competition for space with *S. noctilio*. Population and community-level studies may need to be conducted on parasitoids and siricids before *S. noctilio* establishes in an ecosystem. Lastly, relatively little is known about the natural history of parasitoids including their life-cycle, phenology, host finding abilities through chemical, physical, and auditory cues (but see Bryant 2010), and their effects on native siricids (e.g., that of *S. cinctipes*, *I. montana*, and *R. howdenorum*). All of these areas may be rich and fertile areas for survey and research on hymenopteran parasitoids of siricids in North America. We conclude that it is only through long-term and species-level observational and experimental work on hymenopteran parasitoids that we may start disentangling the biology and ecology of this fascinating and ecologically important group in our native forest stands.

Acknowledgments

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